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INVITED REVIEW

What is a weapon?

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Synopsis Animals utilize an incredible array of traits for offence and defence during conflict. These traits range from exaggerated morphological structures such as the antlers of stags and the horns of beetles, to an arsenal of noxious chemicals emitted, secreted, and injected. However, the breadth of these traits appears to be underappreciated in our current thinking about aggression in animals. Use of the term "weapon" in the current literature is largely restricted to studies of conspicuous morphological structures used by males during contests over access to females, and as a result, our understanding of other types of weapons is limited. In this article, I explore the diversity of traits utilized by animals to manipulate and control the behavior of other individuals in a number of agonistic contexts, with the aim to encourage a reappraisal of the way in which behavioral and evolutionary biologists view animal weapons. I discuss the advantages of including this broader range of traits in studies of animal weaponry and explore the unifying features that distinguish animal weapons from other traits.

Introduction

The term "weapon" is used to describe a whole host of offensive and defensive items used during human conflict. From guns and knives, to explosive, chemical, and nuclear weapons capable of causing extensive damage. Human weapons are often developed specifically for use in conflict but can also be "weapons of opportunity," tools that have been adapted from their original purpose to threaten, manipulate, or damage another individual (e.g., hands curled into fists, wrenches, hockey sticks). Weapons are utilized by humans under a range of different circumstances from hunting to sports, to one-on-one fights, gang violence, and within inter-state wars. However, some of the most elaborate weapons have not been created by human technology but rather through the process of evolution. Animal weapons are equally if not more diverse than those constructed by humans, encompassing exaggerated morphological structures such as the antlers of stags and the horns of beetles, chemical emissions that alter the behavior of their recipient (e.g., the potent spray of bombardier beetles) and toxic injections (i.e., venom).

Animal weapons are used in a variety of contexts including predator defence and prey capture, colony defence, female coercion, and agonistic contests. However, the way in which the word "weapon" is currently used in the literature does not reflect this diversity. A search for the terms "animal AND weapons" using Web of Science results in a total of 67 relevant papers (see Supplementary Appendix for details on how relevance was determined), of which 90% focus on morphological traits and 93% examine the use of weapons only in the context of a dyadic contest (Table 1; see Supplementary Appendix for complete results of literature search). A dyadic contest is an agonistic interaction in which two individuals of the same species (usually males) compete over access to, or ownership of, an indivisible resource (usually food, territory, or a mate). This literature search suggests that animal weapons are restricted to morphological structures used by individuals only during traditional dyadic contests, and while some weapons fit these criteria, as outlined above, many do not. The way in which we use terminology in scientific communications has a significant impact on readership and, moreover, on the ability of researchers to utilize the literature in order to place their research into a broader context. Whether as a direct consequence or not, the wider range of traits used as weapons appear to be

Table 1 Results of Web of Science search for the terms "animal AND weapon"

Class	Prop. of studies
Actinopterygii	0.03
Amphibia	0.01
Anthozoa	0.03
Arachnida	0.01
Aves	0.01
Crustacea	0.27
Insecta	**0.51**
Mammalia	0.10
Reptilia	0.01
Context	
Colony defence	0.01
Dyadic contest	**0.93**
Female control	0.01
Conflict	0.01
Predator defence	0.01
Prey capture	0.01
Structure	
Chemical	0.12
Morphological	**0.90**
Function	
Display	0.16
Injure	0.46
Physically displace	0.39
Manipulate (other)	0.01
Not specified	0.28

Note: The search produced 67 relevant studies. Note that some proportions within the categories are >1.0 due to some studies encompassing more than one of the sub-categories, for example, chemical and morphological weapons. Proportions over 0.5 are highlighted in bold.

underappreciated in our current thinking about aggression in animals. For instance, the several review papers currently available on animal weapons focus entirely on morphological weapon traits (Berglund et al. 1996; Emlen 2008; Tobias et al. 2012; McCullough et al. 2016). This focus on morphology means we are at risk of overlooking the possibility that a greater diversity of traits could have evolved due to similar selection pressures.

The fact that the term "weapon" is heavily biased toward morphological structures and dyadic contests is likely largely due to human visual bias. Morphological weapons are often impressive, exaggerated structures used during dramatic attacks in dyadic contests. The clashing of antlers during rutting season, for example, can not only be seen but also heard and thus attracts attention. Furthermore, conspicuous morphological weapons that double as sexual ornaments have become key traits studied by evolutionary biologists in order to understand evolutionary arms races and life history trade-offs (e.g., Robinson et al. 2006; Simmons and Emlen 2006; Yamane et al. 2010; McCullough and Emlen 2013). As a result, morphological weapons have been studied extensively in the context of dyadic agonistic contests, leading to a greater understanding of their evolution and functional capacities (Emlen 2008). However, the same cannot be said for other weapon traits. In the several reviews available on animal weaponry, chemical weapons are either mentioned only briefly, or overlooked entirely (Berglund et al. 1996; Emlen 2008; Tobias et al. 2012; McCullough et al. 2016), while traits used in offence or defence outside of the context of dyadic contests are not mentioned at all.

The restriction of the term weapon to morphological traits used in dyadic contests may have been driven by the lack of an appropriate biological definition that outlines the key features of animal weapons and thus enables the distinction of weapons from other traits. For instance, although several studies include definitions, these definitions generally define weapons in a particular behavioral context, male–male contests over access to females (Huntingford and Turner 1987; Emlen 2008; Pradhan and Van Schaik 2009; McCullough et al. 2016) (Table 2). These definitions thus cover only a small range of weapons that are indeed morphological features, structures, or outgrowths used in male–male competition, but as described above, not all weapons fit these criteria (Table 3). Traits used by animals in offence and defence vary across four main axes: mode of action (how they are used), context (when they are used), form (what kind of trait they are), and evolution (how they evolved and whether they are specialized or adapted from their original purpose). In this article, I will explore these four axes of variation, with the aim to shed light on the incredible diversity of animal weapons while exploring the shared features that distinguish weapons from other traits.

Mode of action

One of the first things that comes to mind when we think about weapons—and indeed a shared element among definitions of human weapons—is injury. Emlen (2008) noted that the most elaborate weapons are rarely the ones that inflict damage. However, while this appears to be true for morphological weapons (see below), it is not true for other forms. For example, many sea anemones including the

Table 2 Current biological definitions of the term "weapon" (sourced in February 2018).

Source	Definition(s)
Emlen (2008)	"...Structures that are used in combat with rivals over access to females."
	"An arsenal of outgrowths that function in male-male combat."
Huntingford and Turner (1987)	"Strong, hard structures."
	"... used in fights to both maintain contact between the opponents and to push, batter or gore an opponent."
McCullough et al. (2016)	"For the purpose of this paper, a morphological feature that is directly used in male-male fights."
Pradhan and Van Schaik (2009)	"...sexually dimorphic traits that directly enhance the success in contest or combat and also include body size because mere body size also affects this success."

beadlet sea anemone *Actinia equina* possess two different kinds of stinging structures—feeding tentacles and acrorhagi—used to injure other individuals. Although both structures possess harpoon-like stinging cells (nematocytes), the way in which these cells affect their targets is very different. Nematocytes in the feeding tentacles ensnare prey, injecting them with a variety of paralysis-inducing toxins (Halstead 1971; Sher et al. 2005). However, as in many venomous species, *A. equina* are immune to their own toxins and thus these tentacles cannot be used during intraspecific conflict over territory. Instead, *A. equina* deploy acrorhagi, bright-blue vesicles that encircle the oral disc. The nematocytes within these acrorhagi do not inject toxins into their recipients but instead appear to induce the harmful local production of reactive oxidative species, thus circumventing the problem of immunity in order to inflict injury (Bartosz et al. 2008). A further example of injury caused by an elaborate chemical weapon can be seen in the neotropical termite *Neocapritermes taracua* (and in some species of ants—see Davidson et al. 2007, 2012). As termite workers age and their efficiency decreases, they develop "exploding backpacks" in the form of two blue crystalline structures within their abdomens, used to protect the colony. When the colony is attacked, these crystalline structures rupture, releasing a toxic substance that kills both the worker and the intruders (Šobotník et al. 2012).

As well as being used to inflict injury, weapons are regularly (and in some species, more commonly) used as non-injurious signals of strength, dominance, and quality. For instance, the antlers of deer, the enlarged major claw of fiddler crabs, and even the powerful dactyl club of mantis shrimp are all used in non-injurious displays of strength (Clutton-Brock 1982; Jennions and Backwell 1996; Green and Patek 2015), despite their potential to inflict significant damage onto the opponent. In fact, the majority of contests between stags are settled through roaring matches and visual inspection, without any physical contact at all (Clutton-Brock and Albon 1979). By making information about their fighting ability or resource holding potential (RHP) publicly available, individuals are able to dissuade potential rivals from attacking, and thus signaling RHP using weaponry can be a form of defence as well as offence.

Weapons play a number of other defensive roles. Firstly, and perhaps most obviously, weapons can be used to physically block the attacks of opponents. For example, in species that possess horns, antlers, or mandibles, escalation of a fight into physical contact often results in opponents locking their weapons together. This act enables rivals to push and shove each other, demonstrating their strength, with minimal risk of physical damage. Offence and defence are generally accomplished by the same weapon, but some animals have even evolved specialized defensive structures that function alongside their offensive weaponry to prevent injurious fights. For example, males of the horned weevil *Parisoschoenus expositus* have evolved deep sheaths inside their prothoraxes into which each opponent inserts one of its horns during grappling matches (Eberhard et al. 2000), allowing individuals to wrestle with minimal risk of injury.

Weapons can also be used to directly prevent an opponent from gaining access to a contested resource. In the dimorphic dung beetle *Onthophagus acuminatus*, only large-horned males are able to successfully defend their burrows, and the females inside them, by using their horns to block the entrances from rivals (Eberhard 1979; Emlen 1997). Similarly, in several species of termite, soldiers have evolved enlarged plug-shaped heads that are used to block the colony entrance during an attack, preventing access to the vulnerable brood inside (Matsuura 2002; Roux et al. 2009). Finally, animal weapons may also enable individuals to withdraw from a costly conflict. For instance, in a small proportion of fights between female parasitoid wasps *Goniozus legneri*, losers emit a volatile chemical just before fleeing. Exposure to this chemical has detrimental effects on the winner,

Table 3 Examples of the variety of animal weapon traits utilised in different agonistic contexts

Group	Species	Trait	Context(s)	Form	Mode(s) of action: Direct harm	Mode(s) of action: Other disruption	Source
Amphibia	Hylid frog, *Corythomantis greeningi*	Venomous head spines	Predator defence	Chemical/morphological	✓	X	Jared et al. (2015)
Anthozoa	Beadlet sea anemone, *Actinia equina*	Acrorhagi	Dyadic contests over territory	Chemical	✓	X	Bigger (1980, 1982)
Gastropoda	Sea hares, *Aplysia*	Ink secretion	Predator defence	Chemical	X	Blocks predator's chemosensors	Love-Chezem et al. (2013)
Insecta	Bed bug, *Cimex lectularius*	Intromittent organ	Female coercion	Morphological	✓	Prevent female resistance	Stutt and Siva-Jothy (2001)
	Bombardier beetles, *Brachinus*	Chemical spray	Predator defence	Chemical	?	Causes predator to drop beetle	Eisner and Dean (1976)
	Camel cricket, *Pristoceuthophilus marmoratus*	Enlarged hind tibia with femoral spines	Dyadic contests; Female coercion	Morphological	✓	Grasping and pinning opponent/female	Haley and Gray (2012)
	Gall-forming aphid, *Quadrartus yoshinomiyai*	Wavy, adhesive secretion	Colony defence	Chemical	✓	Restricts movement of attacker	Uematsu et al. (2007, 2010)
	Horned weevil, *Parioschoenus expositus*	Sheaths in prothorax	Dyadic contests	Morphological	X	Prevents opponent from inflicting injury	Eberhard et al. (2000)
	Neotropical termite, *Neocapritermes taracua*	Explosive blue crystalline structures	Colony defence	Chemical	✓	X	Šobotník et al. (2012)
	Paper wasps, *Polistes*	Sting	Dyadic contests, predator defence	Chemical	✓	X	Tibbetts and Shorter (2009)
	Parasitoid wasp, *Goniozus legneri*	Volatile chemical	Female–female dyadic contests	Chemical	✓	?	Goubault et al. (2006), Mesterton-Gibbons et al. (2017)
	Queenless ant, *Dinoponera quadriceps*	Chemical marker	Dominance contests	Chemical	✓	Elicits attacks from lower rank females	Monin et al. (2002)
	Termite, *Reticulitermes speratus*	Englarged plug-shaped head	Colony defense	Morphological	X	Block access to colony	Matsuura (2002), Roux et al. (2009)
	Tree Weta, *Hemideina crassidens*	Enlarged mandibles	Dyadic contests; female control	Morphological	✓	Throw female out of gallery after mating	Kelly (2006, 2008)
	Water strider, *Gerris incognitus*	Abdominal claspers and leg spines	Female coercion	Morphological	✓	Force mating; prevent female resistance	Arnqvist and Rowe (1995)
Mammalia	Striped skunk, *Mephitis mephitis*	Noxious chemical secretion	Predator defence	Chemical	✓	X	Wade-Smith and Verts (1982), Lartviere and Messier (1996), Wood (1999)

? = currently unknown

allowing the loser to make its exit unscathed (Goubault et al. 2006, 2008; Mesterton-Gibbons et al. 2017).

Context

All of the functions described above serve to influence the behavior of an opponent in one way or another, be it to deter or defend against an attack or to elicit retreat. Although current literature restricts the use of the term weapon to traditional dyadic contests, individuals utilize traits in order to manipulate the behavior of others in a number of different contexts.

For example, although not traditionally thought of as weapons, traits used during male–female interactions function to directly impose restrictions (usually by males) on the behavior of another individual (usually a female), often by inflicting damage. In fact, many of these structures are the very same traits that are described as weapons when used during male–male contests. For example, male camel crickets *Pristoceuthophilus marmoratus* not only grapple rival males with enlarged femoral spines on their strongly bent hind tibia during duels, but also use these weapons to grasp and pin females, restricting their movement in order to force copulation (Haley and Gray 2012). Similarly, a male tree weta *Hemideina crassidens* will employ his enlarged mandibles to bite and wrestle opponents and also to throw a female out of his gallery once copulation is complete, securing his fertilization success by ensuring that the female does not re-mate with the next male to commandeer his territory (Kelly 2006, 2008).

Males of some species possess specialized structures that are not used during male–male fights but are reserved solely for manipulating females. In their most extreme form, these traits have become known as traumatic intromittent organs and easily rival traits traditionally thought of as weapons in terms of their complexity, diversity, and capacity to damage other individuals. Traumatic intromittent organs have two main functions: (1) to force mating—traumatic intromittent organs are used to pierce the female epidermis, injuring the female, in order to achieve sperm transfer, either through the intromittent organ itself or via another route while the female is anchored (see Lange et al. (2013) and Reinhardt et al. (2015) for reviews of this subject) and (2) to prevent females from remating by inflicting harm (Johnstone and Keller 2000). Furthermore, traumatic mating strategies can have detrimental fitness consequences for females, as a direct result of the damage caused, which in turn lead to evolutionary arms races between the offensive structures of males and the defensive capabilities of females (e.g., water striders *Gerris incognitus*—Arnqvist and Rowe 1995; bed bugs *Cimex lectularius*—Stutt and Siva-Jothy 2001; Morrow and Arnqvist 2003).

Although parallels have been drawn between courtship displays and fighting behavior (Mowles and Ord 2012; Briffa 2015), similarities between traits used to manipulate individuals during sexual conflict and dyadic contests are yet to be considered even though these two forms of conflict possess similar dynamics. Both scenarios involve two individuals that value an indivisible resource: in traditional contests, this resource may be a territory or a mate, whereas in the case of sexual conflict, the contested resource is the female's eggs. Traditional contests involve a series of decisions in which participants weigh the costs and benefits of persisting in the fight or retreating, and the decisions of each individual are influenced by the actions of its opponent (e.g., attacks). Similarly, female harassment/coercion relies on the male increasing the costs of female resistance until she has no choice but to comply and relinquish the resource (i.e., mates with him). Thus it would benefit individuals in both scenarios to be able to manipulate the behavior of their opponent and the costs they must pay to persist (in the case of contests) or resist (in the case of sexual conflict).

Weapons also function in interspecific conflicts such as prey capture and predator defence. Vertebrates utilize a suite of morphological weapons such as teeth and claws in order to catch prey, whereas invertebrates largely employ chemical tactics to escape predation. Sea hares *Aplysia*, for example, secrete ink when under attack by predators. This ink acts as a defensive mechanism via two different routes: (1) it is an unpalatable repellent and (2) it blocks the chemosensory apparatus of the predator, reducing its ability to detect prey, enabling the sea hare to escape (Love-Chezem et al. 2013). Similarly, bombardier beetles of the genus *Brachinus* deter predators by ejecting a potent chemical spray from abdominal glands, which causes the predator to drop the beetle (Eisner and Dean 1976).

Form

Although the majority of studies on animal weapons focus on morphological traits, due to their conspicuous nature, a weapon's visibility does not determine its potency and in fact, as we have already seen, subtle weapons often have more extreme effects on their victims. Chemical weapons act by transferring toxic substances either externally via emission or secretion or internally by injection and are often (but not exclusively) employed by smaller animals such as arthropods. From the perspective of humans, the most infamous Hymenopteran weapon is the injection of venom through a modified ovipositor or stinger (Tibbetts and Shorter 2009), but stinging is just one example of the plethora of chemical weapons employed by Hymenoptera. For instance, the alpha female of the queenless ant *Dinoponera quadriceps* uses a more complex weapon to punish those that try to challenge her. When faced with a rival female, the alpha marks her opponent with a chemical that elicits lower ranking females to punish the rival, biting and holding onto her appendages for up to 4 days (Monin et al. 2002). In this case, the chemical marking itself is perhaps not directly a weapon, but its application to the beta female provokes an injurious response from the other females and thus the alpha's use of this marker is somewhat akin to placing a tracker onto a missile target. Chemical weapons are not limited to Hymenoptera and examples can be seen in aphids, cnidarians, reptiles, amphibians, and even mammals (e.g., platypus). Workers of the gall-forming aphid *Quadrartus yoshinomiyai*, for instance, sacrifice themselves during colony attacks by secreting a waxy substance that acts as an adhesive, gluing the workers to the intruders, preventing further advancement into their territory (Uematsu et al. 2007, 2010). Amphibians rely heavily on chemical defences to avoid being eaten. Aposematic amphibians such as poison dart frogs secrete noxious chemicals directly through their skin (Summers and Clough 2001; Darst et al. 2006), whereas other amphibians transfer toxins using specialized spiny outgrowths (e.g., Brazilian hylid frogs *Corythomantis greeningi* and *Aparasphenodon brunoi*—Jared et al. 2015), or in the case of spanish ribbed newts *Pleurodeles waltl*, co-opted ribs (Heiss et al. 2010).

Although chemical weapons usually require a morphological structure in which to be housed, the injurious effects of morphological and chemical weapons differ significantly. The purpose of a morphological weapon during an attack is to push, pierce, or bruise the epidermis of the opponent, while chemical weapons transfer toxic, often times debilitating substances. However, both weapon types share an ultimate purpose to manipulate individuals and elicit retreat or submission.

Evolution

Some of the weapon traits described above have evolved specifically to manipulate the behavior of others through force or injury. The acrorhagi of anemones, for instance, serve no other function than to injure competitors. But many animal traits have been co-opted from their original purpose for use as weapons. The line between specialized and co-opted weapon traits is somewhat ambiguous as many co-opted traits have since evolved specialized adaptations to increase their efficacy as weapons. For example, the primary purpose of male *P. marmoratus* hind legs would have been locomotion, but these legs have since been co-opted for use in fights and female control, becoming enlarged and developing femoral spikes (Haley and Gray 2012).

The use of co-opted traits as weapons, alongside the fact that many weapons serve a dual function as sexual ornaments, means that weapons are often subject to multiple competing selection pressures. Many weapons are subject to both natural and sexual selection, some at different evolutionary stages—for example, weapons that evolved initially for use in predator–prey interactions (natural selection) but have since been co-opted for use during contests over mates (sexual selection)—while some weapons face multiple selection pressures at once. For instance, the possession of enlarged major claws by male fiddler crabs not only increases fighting ability and mating success, but also increases metabolic demands while simultaneously decreasing male foraging ability (Weissburg 1992; 1993; Levinton et al. 1995). If males are unable to compensate for these costs, the fitness consequences will cause these enlarged claws to become the subject of natural selection in conjunction with the sexual selection already imposed on them by male–male competition and female mate choice.

Traumatic intromittent organs and other male coercive structures directly increase male reproductive success and thus evolve as a result of sexual selection. Although females that mate with good coercers can benefit indirectly by passing on these coercive abilities to their sons, the evolution of female resistance traits provides direct benefits by reducing the amount of harm the females incur and will thus be favored by natural selection (Linder and Rice 2005). This example demonstrates that offensive and defensive weapons utilized within the same interaction can be subject to different selective forces, which due to their opposing directions, ultimately result in an evolutionary arms race. Whether or not similar evolutionary patterns are demonstrated in traditional offensive and defensive weapons however remains to be explored.

Concluding remarks and future directions

The above discussion highlights the immense variety of traits utilized by animals for offence and defence during conflict. These traits vary in terms of the function they perform (e.g., inflicting injury, signaling dominance, deflecting attacks), the context in which they are used (e.g., dyadic contests, sexual conflict, predator–prey interactions), their form (morphological or chemical), and the selection pressures that have driven their evolution. However, despite these differences, all of the traits described here (including traditional animal weapons and traits not traditionally thought of as weapons) share a common ultimate function to constrain the behavior of another individual, either through direct harm or other physical disruption. I would thus argue that this unifying feature distinguishes animal weapons from other traits and therefore that any trait used by an animal to fulfil this ultimate function could be referred to as a weapon. To date, our view of what characterizes a weapon has largely been driven by our human visual bias, resulting in 90% of studies focussing on exaggerated morphological traits such as antlers and horns. Furthermore, the use of the term weapon has been restricted to traits used in the context of dyadic contests even though such contests represent just one example of the conflict generated through natural and sexual selection. This particular aspect is surprising if we consider the number of different types of conflict studied by evolutionary biologists (e.g., pre- and postcopulatory sexual conflict, parent–offspring, predator–prey, sibling rivalry, interspecific conflict over territory and resources) and more so if we think about the variety of contexts in which human weapons are used.

Emlen (2008) stated that "the most glaring void in our understanding of animal weapon evolution concerns the mechanisms generating diversity in weapon form." In order to answer this question fully, it is vital that we (1) understand what the term weapon means and (2) incorporate all traits (i.e., all weapon forms) that fit this definition into studies of weapon evolution. Including weapon traits that share the purpose of constraining the behavior of others but that differ in form, mode of action, and the context within the same studies will shed light on whether these diverse traits are driven by similar evolutionary forces, or whether the specific context or mode of action they are used for elicits divergent pressures. Finally, broadening our use of the term weapon to describe traits utilized in different conflict contexts will encourage new inter-disciplinary collaborations, which in turn will deepen our understanding of the evolution of social behavior and conceivably of parallels between animal and human conflict.

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Supplementary Data

Supplementary Data available at *ICB* online.

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